Some Observations on the Onychophoran Fauna of Tasmania

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ABSTRACT

At least nine species of Peripatopsidae (Onychophora) are native to Tasmania. The four currently recognized viviparous species, all endemic, have 15 pairs of legs and are restricted to northeastern or southwestern parts of the main island: *Tasmanipatus anophthalmus* and *T. barretti* are only found in the North East, and two species of a new genus (as yet undescribed) mainly occur in the South West's World Heritage Area (WHA). All other known species are oviparous, have 14 pairs of legs and were previously identified as *Ooperipatellus insignis*, found in Victoria on the Australian mainland. Egg-laying Tasmanian Onychophora are widely distributed and sometimes locally abundant. Taxonomic characters for oviparous species are here reviewed and it is suggested that "*O. insignis*" in Tasmania is in fact a group of endemic species.

RÉSUMÉ

Observations sur la faune des onychophores de Tasmanie.

Neuf espèces au moins de la famille Peripatopsidae (Onychophora) sont originaires de Tasmanie. Les quatre espèces vivipares connues, toutes endémiques, sont munies de 15 paires de pattes ; elles montrent une distribution restreinte : *Tasmanipatus anophthalmus* et *T. barretti* ont été exclusivement trouvées dans le Nord-Ouest et deux espèces d'un nouveau genre (inédit) existent surtout au South-West's World Heritage Area (WHA). Toutes les autres espèces connues sont ovipares et possèdent 14 paires de pattes. On les a regroupées jusqu'à présent sous l'espèce *Ooperipatellus insignis*, trouvée à Victoria sur le continent australien. Les Onychophores ovipares de la Tasmanie présentent une large répartition et abondent parfois en certains endroits. Ce travail propose une révision des caractères taxinomiques et suggère que "*O. insignis*" représente en fait un groupe d'espèces endémiques de Tasmanie.

INTRODUCTION

Onychophora frequently appear in phylogenetic discussions of the Arthropod relationships, and in zoogeographic discussions of the Gondwanan element in fauna of the Southern Hemisphere. Despite the scientific importance of the group onychophoran taxonomy, especially at the species level, is far from satisfactory (RUHBERG, 1992). This is particularly true for the Onychophora of Tasmania. Although the first record of a Tasmanian species was published 100 years ago (SPENCER, 1895), very little collecting and no taxonomic studies were carried out over the following 80 years. A "boom" in Tasmanian onychophoran research began

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with a visit to the island by Dr. V. van der LANDE in 1977. The present authors and their colleagues have been studying the Tasmanian fauna since the mid-1980's, and considerable progress has been made towards a comprehensive monograph (RUHBERG & MESIBOV, in prep.).

TASMANIA - A SPECIAL ISLAND

Global climatic changes and other events have resulted in Tasmania being separated from the Australian continent on several occasions during the past 2.5 million years. Australia itself is an isolated remnant of Gondwana and thus is rich in ancient groups of its flora and fauna with high percentage of endemisms (SMITH *et al.*, 1993). Tasmania experienced several highland glaciations during the Pleistocene (DARLINGTON, 1969). The present isolation as an island is believed to have stabilized some 6000 years ago. Cooling factors peculiar to this island together with isolation periods resulted in the evolution of numerous taxa of plants and animals which are now endemic to Tasmania, and has made this island an important repository and refuge for archaic elements of great biological interest and significance. Amongst these are the Onychophora, commonly referred to as "*Peripatus*", "Velvet Worms" or "Living Fossils".

HISTORY OF ONYCHOPHORAN RESEARCH IN TASMANIA

A "rather bleached specimen with fifteen pairs of legs" in the Macleay Museum in Sydney was first noted by FLETCHER (1890) as demonstrating "the occurrence of '*Peripatus Leuckarti*' in Tasmania". Unfortunately this specimen no longer exists in the museum's collections (D.S. HORNING, pers. comm., 1994), and nothing more is known of its morphology or provenance.

Three years later, Sir Baldwin SPENCER collected some 15 specimens of what he called "*Peripatus insignis* " at Dee Bridge in south central Tasmania (SPENCER, 1895). *Peripatus insignis* was the name which had been given by DENDY (1890) to the second only known oviparous onychophoran described from Macedon, Victoria on the Australian mainland. Both the Victorian and Tasmanian specimens had 14 pairs of legs. However, SPENCER (1895) mentioned differences in size between the mainland and the Tasmanian form. DENDY (1900) erected the genus *Ooperipatus* to contain *all* oviparous Australian Onychophora, regardless of whether they had 14 or 15 pairs of legs. In his famous monograph on the oviparous species of Onychophora, he himself laid the foundation for future taxonomic confusion when he synonymized the Victorian *Ooperipatus insignis* from Macedon and the Tasmanian "*insignis* " from Dee Bridge (DENDY, 1902: 403, 408).

A note by BAEHR (1977) on Australian Onychophora included the description of a new species with 14 pairs of legs, *Ooperipatus decoratus*, from Dip Falls in northwestern Tasmania. The type material, thought until recently to be missing, has now been relocated and re-examined by the senior author.

Following a collecting trip to western Tasmania in 1977, Dr. V. van der LANDE requested additional material from Dr. J. HICKMAN of the University of Tasmania, as a form with 15 pairs of legs among her specimens could obviously *not* be identified as *Ooperipatus insignis*. Her request encouraged local zoologists to deliberately search for Onychophora. In 1983, Leigh WINSOR (unpublished report) noted the occurrence of a form with 15 pairs of legs, which he called "*Peripatoides leuckarti* ", near the Franklin River in the South-West (MALCOLM, 1987). A second form with 15 pairs of legs from northeastern Tasmania, was found by the junior author in 1984, and was later described as *Tasmanipatus barretti* together with a third species, *Tasmanipatus anophthalmus* by RUHBERG *et al.* (1991). At the same time, in 1984, the senior author was completing a revision of the Peripatopsidae of the world, and had available for study only 18 preserved museum specimens from Tasmania, all of them in rather bad condition. Accordingly the results were tentative and indicated a need for further work on fresh material. RUHBERG (1985) retained the genus name *Ooperipatus* for its generotype *Ooperipatus oviparus*

(a larger oviparous form with 15 pairs of legs from Victoria) and erected a new genus: *Ooperipatellus*, to contain all remaining oviparous species with 14 pairs of legs. She considered the meagre Tasmanian material in hand to be conspecific with two redescribed and renamed species from the Australian mainland: *Euperipatoides leuckarti* (SAENGER, 1869), a viviparous form from New South Wales, with 15 pairs of legs, and *Ooperipatellus insignis* (DENDY, 1890), from Victoria, with 14 pairs of legs.

An Australia-wide survey of Onychophora was begun in 1985 by Drs. N. N. TAIT and D. A. BRISCOE following their discovery of New South Wales forms with peculiar head organs (TAIT & BRISCOE, 1990). In 1987, TAIT & BRISCOE collected Onychophora throughout Tasmania, including remote portions of the World Heritage Area in the South-West. These visits, aimed principally at securing material for allozyme electrophoretic investigations (TAIT & BRISCOE, in SMITH *et al.*, 1993), stimulated the junior author to begin intensive field studies of onychophoran conservation (e.g. MESIBOV, 1988, 1990, 1994). The senior author made the first of three visits to Tasmania in 1989, and Dr. D. ROWELL has included recently collected Tasmanian forms in his studies of chromosomal variation and chromosomal evolution within a sample of Australian Peripatopsidae (ROWELL, unpubl. obs.; ROWELL *et al.*, 1995).

As a result of all these recent activities there is now a rich supply of material available for further taxonomic work on the Peripatopsidae of Tasmania enabling the earlier studies to be reassessed. The first questions to be answered are:

(1) Are the Tasmanian species referred to *Euperipatoides leuckarti* and *Ooperipatellus insignis* conspecific with their mainland counterparts?

and:

(2) Are there more species in Tasmania than at present described?

In what follows, we attempt to answer these questions, concentrating on the taxonomic complexities of the oviparous forms. We begin, however, with a brief review of the viviparous species.

VIVIPAROUS TASMANIAN ONYCHOPHORA

All known viviparous[1] forms from Tasmania have 15 pairs of legs in both sexes. Their distributions are remarkably restricted, with one group found only in the North-East and the other in the South-West (FIG. 1a).

One of the northeastern species, *Tasmanipatus anophthalmus* Ruhberg *et al.*,1991, is white and "blind" (RUHBERG *et al.*, 1991; MESIBOV & RUHBERG, 1991). Its congener, *T. barretti* Ruhberg *et al.*, 1991, has obvious eyes and is dorsally pinkish pigmented. The two species occur parapatrically in forest habitats over ca. 1,000 sq. km. (RUHBERG *et. al.*, 1991; MESIBOV & RUHBERG, 1991). Histological investigations have revealed that an "inner" eye occurs in both species, and that *T. anophthalmus* lacks the lens and the retina-pigment found in this structure in *T. barretti* (RUHBERG *et al.*, in prep.).

Viviparous forms from southwestern Tasmania were previously referred to *Euperipatoides leuckarti* (Saenger, 1869), (RUHBERG, 1985). It now seems clear that the southwestern viviparous Onychophora represent two allopatrically distributed species (FIG. 1a) in a new genus, to be described in a forthcoming paper (RUHBERG, in prep.).

In summary, there is now strong evidence from morphological and phylogenetic studies (RUHBERG in prep.; REID, 1995, in prep.), chromosome studies (ROWELL *et al.*, 1995) and allozyme investigations (TAIT & BRISCOE in: SMITH *et al.*, 1993), that *none* of the Tasmanian

1 *All* viviparous Peripatopsidae from Australia are new considered to be ovoviviparous (CAMPIGLIA & WALKER, 1995; REID, pers. comm.).

viviparous species are conspecific, or even congeneric, with mainland Australian forms. All show clear-cut diagnostic features and are further characterized by their geographically restricted distributions.

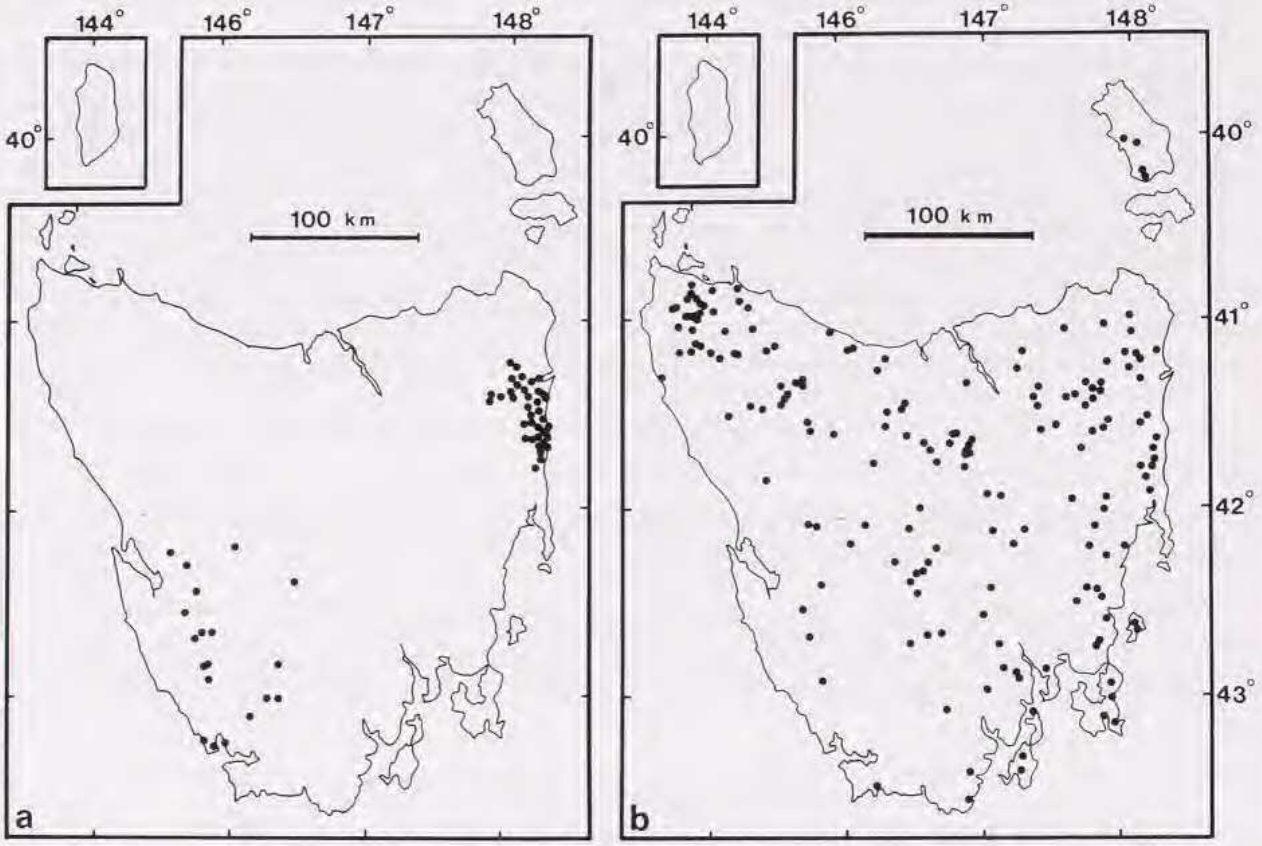

FIG. 1 a-b. — Distribution of (a) viviparous and of (b) oviparous Peripatopsidae in Tasmania.

OVIPAROUS TASMANIAN ONYCHOPHORA

Oviparous forms were previously identified with the Victorian *Ooperipatellus insignis* (DENDY, 1890), (RUHBERG, 1985). Egg-layers are found throughout the main island of Tasmania and on several offshore islands (Fig. 1b). They occur in forest, woodland and scrub habitats from sea level to at least 1,100 m and are sometimes locally abundant. Occurrences in forest after clearfell logging, part-clearing or burning demonstrate that oviparous species, at least in the short term, are remarkably tolerant of habitat disturbance (MESIBOV, unpubl. results).

In contrast to viviparous species in Tasmania, oviparous forms are superficially very similar. All females have a prominent ovipositor and lay shelled eggs (Figs 4e, 3d), all males have a nearly uniform distribution-pattern of crural papillae on leg-pairs 6-13, and both sexes have 14 pairs of walking appendages. These characters are shared by Victorian and New Zealand oviparous species within the genus *Ooperipatellus* which are also alike in having a 2n chromosome number of 42. In contrast there is much variation within the viviparous forms. *Tasmanipatus*- spp. have 2n = 34 or 36 and the yet undescribed viviparous southwestern genus has 2n = 18, with interspecific variation in sex chromosomes (ROWELL *et al.*, 1995).

Early taxonomic studies relied to a large extent upon colour and colour-pattern, as can be seen in DENDY's impressive opus "On the oviparous species of Onychophora" (DENDY, 1902;

pl. 19, Figs 1-3). We have found that colour and colour-pattern *per se* are unreliable characters in onychophoran systematics, and that other traits need to be examined (RUHBERG, 1992).

In an effort to improve the taxonomy of oviparous onychophorans, and to arrive at a well grounded biospecies-concept, the present authors, in collaboration with specialists, are using data on external and internal anatomy, histology and ultrastructure, allozyme electrophoresis, behaviour and distribution patterns. Specimens for these investigations derive almost entirely from our own field collections (mainly deposited in the Queen Victoria Museum and Art Gallery, Launceston, Tasmania), and include animals bred in the laboratory by H. R. in Hamburg. The results of particular studies will be published in forthcoming papers. Here we review progress in identifying species–diagnostic characters.

DIAGNOSTIC CHARACTER VARIATIONS IN OVIPAROUS ONYCHOPHORA

For the sake of completeness we begin with a revision of the genus *Ooperipatellus.*

Ooperipatellus s. str. Ruhberg, 1985.

Type species: *Peripatus insignis* Dendy, 1890 from Macedon, Victoria (to be redescribed in REID, in prep.).

Distribution

Victoria, Tasmania, New Zealand.

Diagnosis

Ooperipatellus is a genus of Australasian oviparous peripatopsid Onychophora with 14 pairs of legs. Females have a prominent ovipositor and lay shelled eggs, males have crural papillae on leg pairs 6-13. Outer jaw blade without accessory tooth.

Differential diagnosis

Ooperipatellus, s. str., is distinguished from all other known oviparous peripatopsid genera on the basis of a unique combination of characters (for comparison see RUHBERG, 1985). It is distinguished from *Ooperipatus,* the "larger Victorian genus" which has 15 pairs of legs, male crural papillae on leg pairs 2-14, and an accessory tooth on the outer jaw blade.

Ooperipatellus is separable from most other currently recognized, but as yet undescribed oviparous mainland Australian species (REID, in prep.), in lacking characteristic head organs. Further the latter forms show different patterns of male crural papillae.

Ooperipatellus nanus Ruhberg, 1985, a tiny form from southern New Zealand, with only 13 pairs of legs, which was previously tentatively assigned to this genus (RUHBERG, 1985: 131) shows more unique characters in adults now than could be deduced from juveniles at hand in 1985. This species has to be transferred to a new genus (RUHBERG, in prep.).

Description

Oviparous peripatopsids. Leg number constant within species, last leg pair well developed, with claws. Foot with 3 distal papillae, no basal papillae. Anal cone of variable length (Fig. 2f, 4a-c). Genital pore in males of variable shape (Figs 4a-c), females with distinct ovipositor of variable length (Fig. 4e).

Males with accessory glands coiled around each other.

Females with paired, flat ovaries, closely attached to the pericardial septum. Ovarial eggs exogeneous and highly variable in size; rudiments of receptacula seminis only present in juvenile females, lost in adults. Additional pouches lacking. Uterine eggs of varying developmental stages.

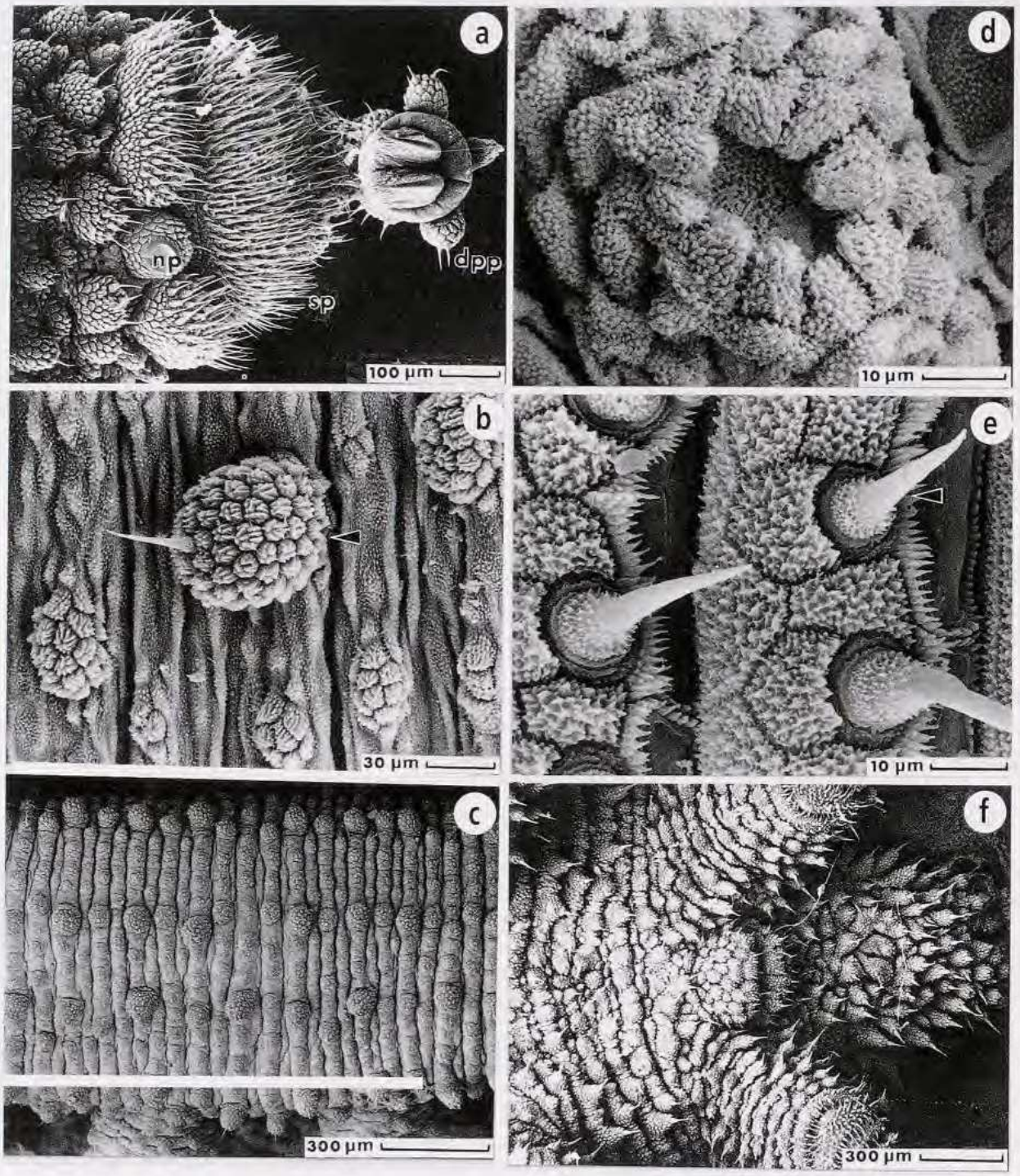

FIG. 2 a-f. — SEMs of Tasmanian Onychophora: (a) Fourth foot with three distal papillae (dpp), nephropore (np) and spinous pads (sp); (b) Dorsal skin with primary (arrowhead) and secondary dermal papillae (a-b, e: *Ooperipatellus* sp. from Black River); (c) Typical pattern of dermal papillae and plical folds in *O. decoratus* ; (d) Yet undescribed structure on dorsolateral skin in *Ooperipatellus* sp. from Christmas Hill; (e) Antennal tip: second and third annulus, each with one row of mechanoreceptors only (arrowhead); (f) *Tasmanipatus barretti*: Hind end of body with a pronounced anal cone.

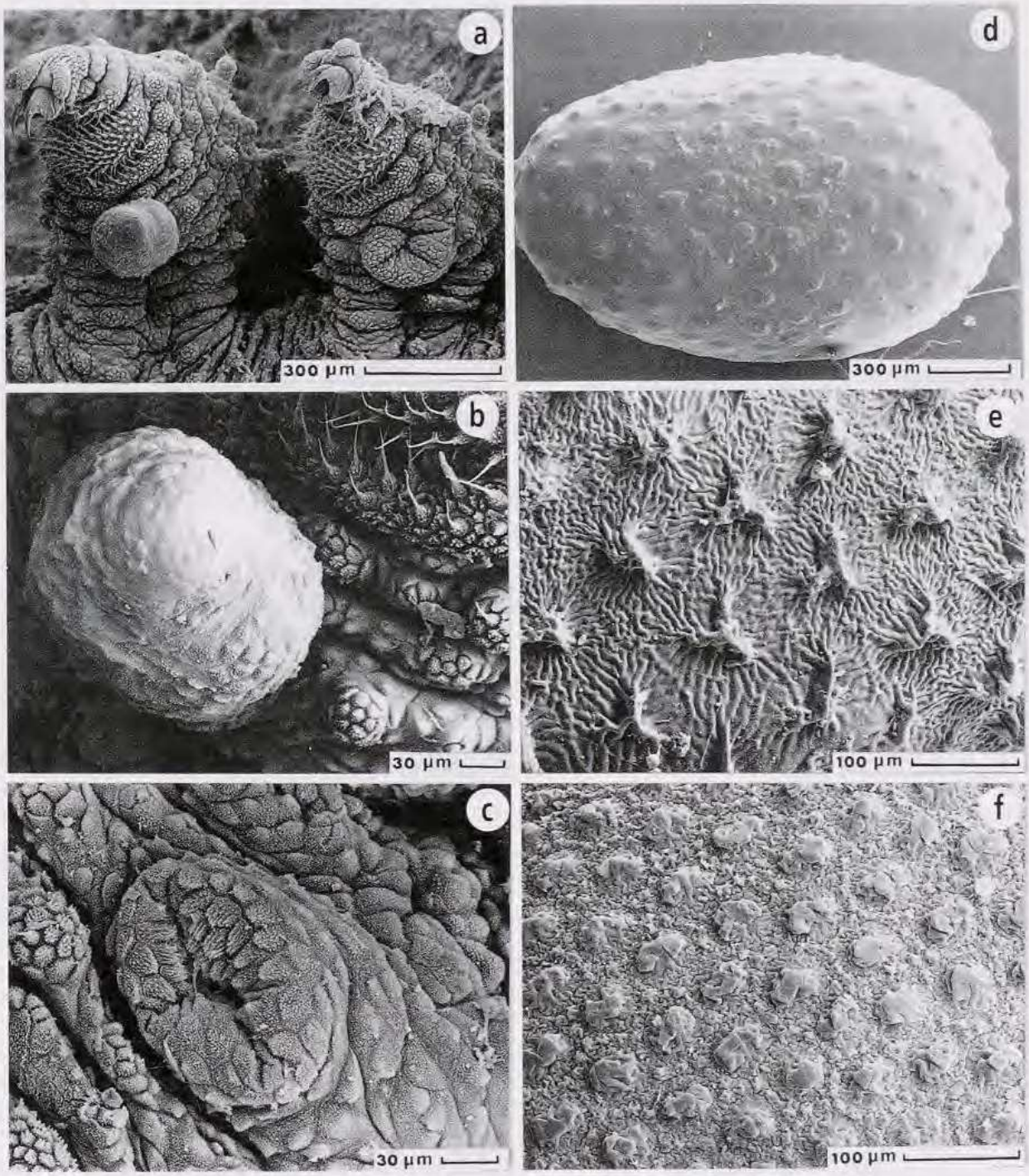

FIG. 3 a-f. — SEMs: (a-b) Different size and shape of male crural papillae in *Ooperipatellus* sp. from Black River: (a) 11th (left on FIG.) and 12th leg (right on FIG.); (b) 7th leg; (c) Crural papilla on 12th leg in *O. decoratus*; (d-f) Chorion of ripe eggs: (d) Egg from a yet undescribed oviparous species from Bellenden Ker. N- Queensland; (e) Sculpture of egg-chorion in *O. decoratus* ; (f) egg-chorion in *Ooperipatus oviparus* from Victoria.

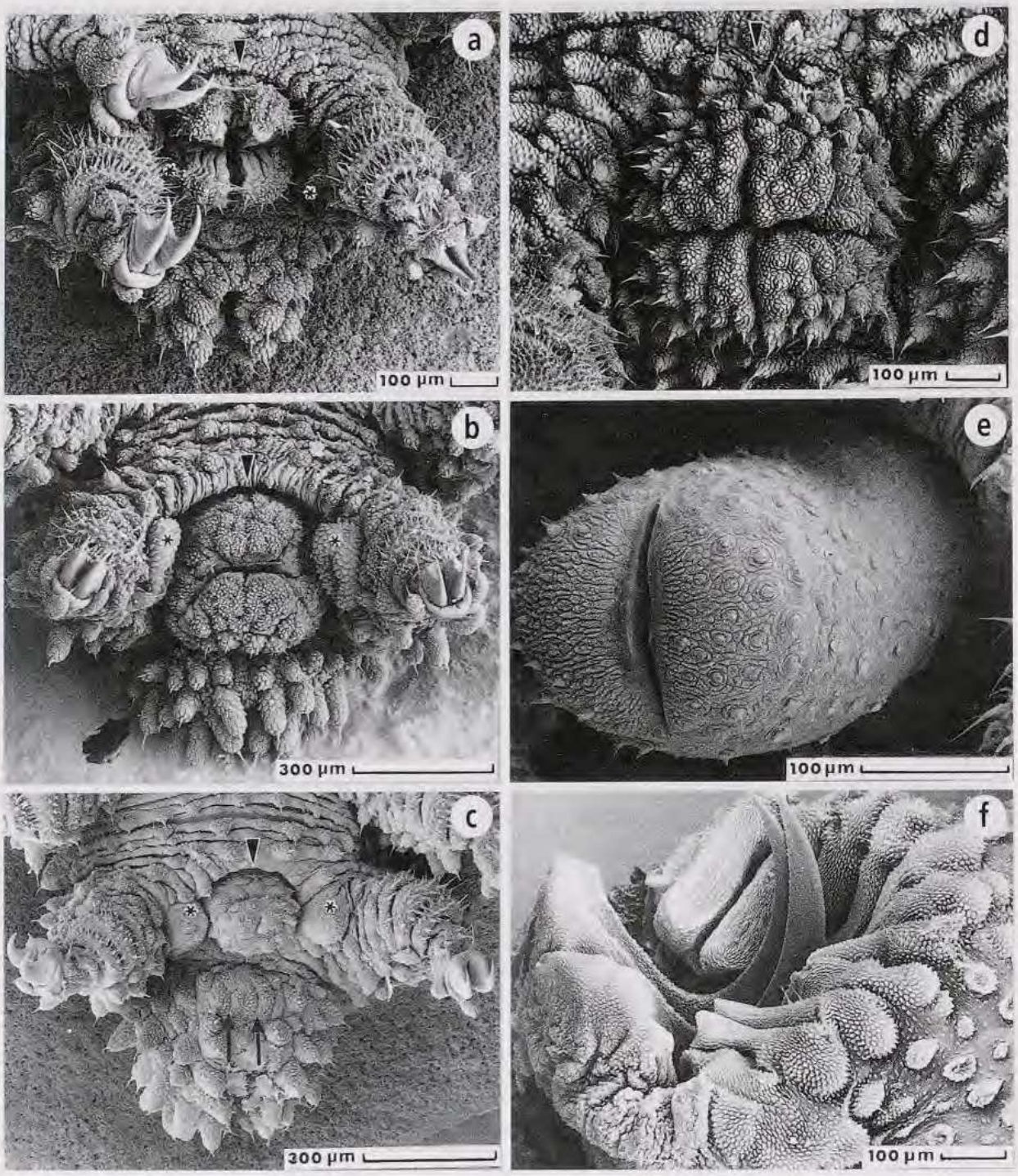

FIG. 4 a-f. — SEMs: (a-c) Different shape and size of genital pores (arrowheads), crural papillae of last legs (asterisks) and anal-slits (arrows) within male oviparous species; (a) Body's hind end in a sexual active *O. decoratus*, collected by R. M. during a "swarming night" in October 1992; (b) *Ooperipatellus* sp. from Black River, Tasmania; (c) *Ooperipatus oviparus* from Victoria; (d) Cruciform male genital pore in the viviparous *Tasmanipatus barretti* ; (e) Ovipositor of *O. decoratus* ; (f) Distinct head organ in a yet undescribed viviparous species from the Tinderry Mts., NSW (lateral view).

Species–diagnostic characters so far recognized in *Ooperipatellus*, are noted below:
External Anatomy; Internal Anatomy; Histology and Ultrastructure; Allozyme Electrophoresis; Behaviour; Distribution; Other Characters.

a) External Anatomy

The number, size, shape and pigmentation of spinous pads of the foot; the position of the nephropore on the 4th and 5th pair of legs; the number, size and arrangement of distal and basal foot papillae (Fig. 2a); the structure and distribution of dorsal skin papillae (Figs 2b-c), the number of dorsal plical folds (Fig. 2c), the presence or absence of as yet undescribed structures on the latero-dorsal surface (Fig. 2d); the size of the primary dorsal papillae (Figs 2b-c), which varies to give an overall "smooth" or "warty" appearance to the body; the number of rows of mechanoreceptors on the second and third distal annulus of the antenna (Fig. 2e); the presence or absence of a deep wrinkle at the antennal base (TAIT & BRISCOE, 1987); the size, shape and position of the male crural papillae on leg-pairs 6-13 (Figs 3a-c, 4a-c), the degree of elongation of the anal cone (Fig. 2f), the degree of reduction of the last legs; and the overall size, e.g. the "stoutness" or the "slenderness" of the body (cf. BOUVIER, 1905; pl. I, Figs 4 & 6).

Coloration characters must be used with care. Even when very distinctive *dorsal* patterns appear in a population (e.g. a "striped", "chequered", "diamond", "chessboard", "spotted", or "speckled" pattern) there can be substantial within-population variation (BROCKMANN, 1994; Figs 7-8). Eye coloration is an unreliable character, it seems to change in fixative. Nevertheless, antennae appear to have species-characteristic patterns of annular coloration which are already visible in late embryos (BROCKMANN, 1994). The occurrence or absence of pigment and/or colour patterns of the *ventral* body surface is characteristic as well and so is the pigmentation of the hatchling in oviparous respectively of the newborn in viviparous species (RUHBERG, pers. observations).

b) Internal Anatomy

Among the anatomical characters are mainly the peculiarities of the genital tracts in both sexes. In *Ooperipatellus*, species can be distinguished by the following characters: the position and shape of male crural glands (within the leg or free in the body cavity) and anal glands (e.g. accessory glands coiled or uncoiled). The structure and development of the ovarial and uterine eggs in the females vary in number and age.

c) Histology and Ultrastructure (SEM, TEM)

The sculpture of the chorion of the ripe uterine or freshly deposited egg (DENDY, 1902; pl. 21; Figs 20-27, and this report, Figs 3d-f) is highly characteristic. Of further taxonomic value are SEM-details of the integument, including the size, shape and number of scales on the main dorsal papillae (Fig. 2b); features of the head, feet and genital region, and as yet undescribed structures in certain species (Fig. 2d) which are currently under investigation with regard to their function and taxonomic value (RUHBERG, in prep.).

First results from histological studies of *O. decoratus* (males, females and eggs) are promising (BROCKMANN, 1994), in that this species shows clear histological differences when compared with *O. insignis*, as described by DENDY (1902). Unfortunately, freshly killed material is needed for such studies and histological characters may not be of use in identifying museum specimens. The same caution applies to use of ultrastructural differences noted in examination of fresh *O. decoratus* and *O. viridimaculatus* (DENDY, 1900; RUHBERG & BROCKMANN, in prep.); among the most valuable TEM-criteria are details of the spermatophores. In contrast, SEM-investigations are possible with old museum material as well (RUHBERG, 1985, 1992).

d) Allozyme Electrophoresis

Characteristic allozyme patterns in Tasmanian oviparous forms have been used by TAIT & BRISCOE (in: SMITH *et al.*, 1993) as the basis for separating taxa in the "*O. insignis*" complex. These "electrotaxa" are tentative, but the patterns suggest, that oviparous forms can have

restricted distributions within Tasmania, and that the Tasmanian forms are only distantly related to oviparous Onychophora on the Australian mainland.

e) Behaviour

Ooperipatellus viridimaculatus from Shennandoah Saddle, New Zealand, South Island, lies still when picked up and is remarkably sluggish in culture (RUHBERG, pers. obs.), while a new *Ooperipatellus* -species from northwest Tasmania (RUHBERG & MESIBOV, in prep.) very rapidly coils itself into a tight helix when disturbed. *O. viridimaculatus* is also unusual in carrying its antennae mostly bent backwards. A curious "swarming" of *O. decoratus* was noted one night in October 1992, when hundreds of individuals were seen climbing trees about an hour after sunset at a field site in northwest Tasmania (MESIBOV, unpubl. obs.). A random sample from the swarm proved to be 90% males, with individuals showing widely opened genital pores (FIG. 4a), and drops and threads of secretion clinging to crural gland openings (RUHBERG, unpubl. obs.). It is not yet known whether any other *Ooperipatellus* species exhibit swarming.

f) Distribution

Onychophoran populations are generally rather small and their distribution is disjunct on both large and small scales. In several places egg-layers occur sympatrically with live–bearers. Within Tasmanian Onychophora all possible distributional patterns do occur: broad sympatry, narrow sympatry, parapatry and allopatry (MESIBOV, unpubl. obs.). A few species seem to be better dispersers than others (e.g. *T. barretti* compared to *T. anophthalmus*). Onychophora in the State have been collected in almost all forest types: dry, wet and alpine. Although oviparous Onychophora are almost ubiquitous in Tasmania (Fig. 1b), it is clear from our preliminary taxonomic work that individual species can be restricted to relatively small areas. It seems unlikely that differing habitat preferences account for range limitation, and in all cases the microclimate parameters are similar in the prefered shelters: under logs and stones, in leaf litter and soil crevices. Distribution limits may be "historically" determined or may be controlled by interactions with other Onychophora, as is suspected to be the case for the parapatric *Tasmanipatus* species of northeast Tasmania (MESIBOV & RUHBERG, 1991). Where range boundaries are sharp, location may be used as a species-diagnostic character.

g) Other Characters

There is potential for using secretions as species-diagnostic biochemical characters. Recently ELIOTT *et al.* (1993) have shown that crural gland secretion in males of the viviparous *Cephalofovea tomahmontis* Ruhberg *et al.*, 1988, acts as a chemoattractant for conspecific females. Extensions of this study to oviparous species may reveal a range of biochemically distinctive, pheromonal attractants. Onychophoran slime may also be taxonomically useful (RENWRANTZ & RUHBERG, in prep.), although the slimes of the *Ooperipatellus*-species so far studied appear to be nearly indistinguishable. Chromosome studies also have so far documented the close relationship of *Ooperipatellus*-species from Tasmania, Victoria and New Zealand (ROWELL, pers. comm.). Onychophora have the right properties (small, isolated populations) for the study of chromosome driven speciation. As has been outlined before there is much variation in the chromosome numbers within the Australian viviparous forms while all oviparous representatives of *Ooperipatellus* investigated are alike in having a 2n = 42 chromosome-number-pattern (ROWELL *et al.*, 1995, in press). The latter is also the largest chromosome number observed to date in Onychophora.

DISCUSSION

Returning to our earlier questions, we are now confident on the basis of morphological and other studies that (1) neither *Euperipatoides leuckarti* nor *Ooperipatellus insignis* is present in Tasmania, and (2) that Tasmania is home to four, not three, viviparous species and to at least five, not one, oviparous species of Onychophora. The oviparous species have congeneric

relatives in Victoria and New Zealand and will be described in forthcoming papers (RUHBERG & MESIBOV, in prep.).

For identification in the field it is convenient that viviparous Tasmanian species all have 15 pairs of legs, while oviparous Tasmanian species all have 14 pairs of legs. Identifications within the taxonomically difficult oviparous group will depend on careful examination of many of the subtle characters noted in this paper, a procedure made more difficult by the absence in the Tasmanian forms of "complicated characters" sensu HENNIG, such as the head organs (Fig. 4f) found in some oviparous and viviparous Onychophora on the Australian mainland (RUHBERG *et al.*, 1988; TAIT & BRISCOE, 1990; REID, in prep.).

Phylogenetic studies of oviparous forms will also be difficult, and a combined morphological, genetic and ecological approach will be the key to understanding their radiation within Australia. The effort will be worthwhile, as it will shed light on whether egg-laying or (ovo-)viviparity is the primitive reproductive mode in the peripatopsid Onychophora. The co-existence of both reproductive modes in Tasmania is both a mystery and an opportunity for understanding the respective advantages of the two strategies.

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